THE SCINCID LIZARD GENUS *NANNOSCINCUS* GÜNTHER: A REVALUATION

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A combination of skeletal, scalation, coloration and reproductive characteristics are used to analyse the intrageneric relationships of the species included in *Nannoscincus* (Sadlier, 1987), which is here shown to comprise 2 subgenera. Proposed is a monotypic subgenus *Nannoseps* n. subgen. for the Australian species *N. maccoyi* (Lucas and Frost). The New Caledonian species *N. mariei* (Bavay), *N. gracilis* (Bavay), *N. sleveni* (Loveridge), *N. rankini* Sadlier and *N. greeri* Sadlier comprise the nominate subgenus. Within the subgenus *Nannoscincus* there appear to be 2 distinct species groups, the *N. mariei* species group (including *N. mariei*, *N. greeri* and tentatively *N. rankini*) and the *N. gracilis* species group (including *N. gracilis* and *N. sleveni*). □ *Scincidae, Nannoscincus, phylogeny, Australia, New Caledonia*

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Greer (1979) diagnosed 3 major lineages for the Australian scincid lizard fauna, the *Egernia*, *Sphenomorphus* and *Eugongylus* groups. These groups are widespread within Australia and also include most scincid genera in the Pacific region. Outside Australia, the *Egernia* and *Sphenomorphus* groups are distributed mainly over the Indonesian archipelago east to the Solomon Islands; members of the *Sphenomorphus* group in particular are prominent in closed forest habitats. By contrast, the distribution of the *Eugongylus* group outside of Australia is mainly over the Pacific islands to the east of Australia (including New Guinea) and is poorly represented in the Indonesian archipelago.

Within the *Eugongylus* group (Greer, 1990) there is a distinct subgroup of species that share a derived character state unique within lygosomine skinks. This subgroup is diagnosed by having the atlantal arches of the first cervical vertebrae fused to the intercentrum. Within this subgroup a subset of species share a pattern of phalangeal reduction on the 4th digit of the manus not observed in other *Eugongylus* group members. This subset of species comprises the genus *Nannoscincus* and includes: *Anotis mariei* Bavay, 1869; *Lygosoma gracilis* Bavay, 1869; *Saiphos maccoyi* Lucas and Frost, 1894; *Lygosoma sleveni* Loveridge, 1941; *Nannoscincus rankini* Sadlier, 1987; *Nannoscincus greeri* Sadlier, 1987. In addition to the pattern of phalangeal loss all members of this subgroup are small (maximum snout to vent length of 50mm in *maccoyi* the largest species) with elongate bodies and reduced limbs which fail to meet when adpressed to the body. They generally occur in closed forest or montane habitats, sheltering beneath and within rotting logs or under stones, or within the fine, loose superficial substrate beneath these sheltering sites.

SYSTEMATICS

Greer (1974) in reviewing *Leiolopisma* and associated species identified 2 groups (Groups II and III of that work) which essentially comprise what is now regarded as the *Eugongylus* group (Greer, 1979). Greer (1974) was however unclear as to whether *Anotis* Bavay (a Group II member at that time comprising the Australian species *A. maccoyi* (Lucas and Frost), *A. graciloides* (Lönnberg and Anderson), and the New Caledonian species *A. mariei* Bavay, *A. gracilis* (Bavay), and *A. sleveni* (Loveridge)) was monophyletic or polyphyletic.

Czechura (1981) noted that *Anotis* Bavay was preoccupied, and resurrected *Nannoscincus* Günther to replace it.

A review of the New Caledonian scincids by Sadlier (1987) redefined *Nannoscincus* largely on the basis of the pattern of phalange reduction in the 4th digit of the manus. *Lygosoma graciloides* with a pattern of phalange reduction in the 1st digit only was removed, and the genus then comprised the species *N. gracilis*, *N. mariei*, *N. sleveni*, *N. rankini*, *N. greeri* and *N. maccoyi*. Note that Greer (1982) further defined *Geomyersia* when describing a second species in the

genus, *G. coggeri;* he listed as one of the diagnostic features a phalangeal formula similar to *Nannoscincus.* Re-examination of *Geomyersia* shows it to have a primitive phalangeal formula and is for this reason not considered further here.

Subsequent research on the species of *Nannoscincus*, particularly osteology and soft morphology, has established the Australian species *Saiphos maccoyi* Lucas and Frost as a sister group warranting subgeneric recognition within a redefined *Nannoscincus* that also recognises the New Caledonian species as a monophyletic subgenus.

METHODS AND MATERIALS

Scalation and reproductive characteristics were assessed on whole alcoholic specimens. Phalange and presacral vertebrae condition were assessed from x-rays of selected samples. Vertebral and sternal characters were assessed from a combination of cleared and stained and whole alcoholic specimens, and skull characters from a combination of cleared and stained and skeletal preparations. Coloration characteristics were determined from my field observations. Polarities for characters, unless otherwise stated, are those used by Greer in determining relationships between lygosomine skinks, otherwise the primitive state is considered the widespread condition in the primitive *Eugongylus* group species. Sources used in assigning character polarities are as follows: character state A, Greer (1974); character state B, this work; character state C, Greer (1974); character state D, Greer (1983); character state E, this work; character state F, this work and Greer (1974); character state G, Lecuru (1968 :524, fig. 8a and 8b); character states H and I, Romer (1956) as cited in Greer (1983); character state J, Hoffstetter and Gasc as cited in Greer (1983); character state K, Romer (1956); character state L, Greer (1987).

Evaluation and Distribution of Characters

The following 13 characters were used in inferring relationships between species of *Nannoscincus.*

A. Prefrontal scales. Primitively the prefrontals of lygosomine skinks are moderately large and either in contact medially or narrowly-moderately separated (A). From this primitive condition the prefrontals can be lost in 2 ways, either through fusion to the frontonasal (a1) or through diminution (a2).

In *N. maccoyi* the prefrontals are absent. Loss of the prefrontal scales through fusion (a1) in *N. maccoyi* is indicated by a single 'anomalous' specimen from Bendigo, Victoria (Fig. 1a) in which the prefrontals are distinct and in broad contact, whereas in all other *N. maccoyi* examined the prefrontals are absent (Fig. 1b) but retain an undulating shape to the frontonasal-

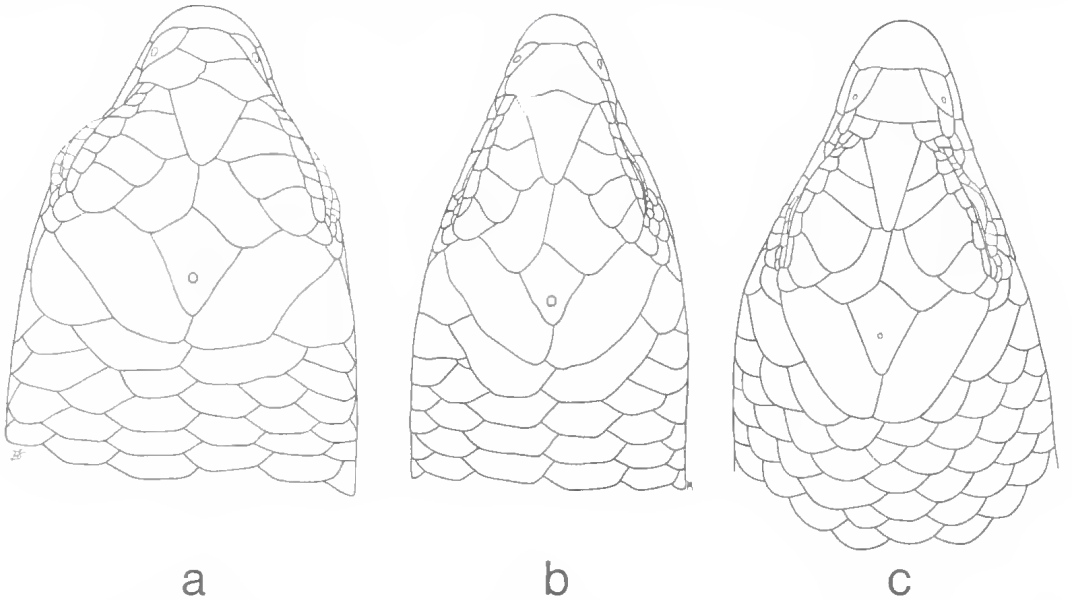


FIG. 1. Dorsal views of the head scalation of: (a) aberrant *N. maccoyi* (note broadly contacting prefrontal scales); (b) lectotype of *Saiphos maccoyi* Lucas and Frost (NMV D1851); (c) *N. mariei.*

frontal suture characteristic of species with well developed prefrontals (and also in the specimen of *N. maccoyi* from Bendigo mentioned above). The prefrontals in the remaining species of *Nannoscincus* appear to have been reduced by diminution (Fig. 1c) as indicated by their small size and obvious separation.

B. Contact between the 1st supraciliary and frontal scales. Contact between the prefrontal and 1st supraocular scales is considered the primitive (B) condition. Contact between the 1st supraciliary and frontal scale, thereby excluding contact between the prefrontal and 1st supraocular is considered derived (b).

Contact between the prefrontal and 1st supraocular occurs in *N. maccoyi*, and *N. mariei*, while *N. gracilis*, *N. sleveni*, *N. greeri* and *N. rankini* generally have the derived condition.

C. Frontoparietal scales. In the primitive condition the frontoparietals are present as 2 distinct scales (C). Fusion of these scales along the midline to form a single scale is considered to be derived (c).

The primitive condition occurs in *N. maccoyi*, *N. mariei*, *N. gracilis*, and *N. sleveni*, while the derived condition occurs in *N. greeri* and *N. rankini*.

D. Loreal scales. The presence of 2 distinct loreal scales between the nasal and preocular scales is considered to be the primitive condition for lygosomine skinks (D). In most primitive lygosomine skinks the anterior loreal is either square or slightly higher than wide, while the posterior loreal is either square or slightly wider than high.

The primitive loreal condition in *Nannoscincus* occurs in *N. gracilis* and *N. sleveni* which have 2 reduced loreal scales (D), the anterior usually present as a semilunar scale positioned on the posterodorsal margin of the nasal and failing to contact the labials, and the posterior usually as high as the nasal but noticeably wider dorsally than basally. *N. maccoyi*, *N. mariei*, *N. greeri* and *N. rankini* all have a single loreal scale which is considered to be derived (d).

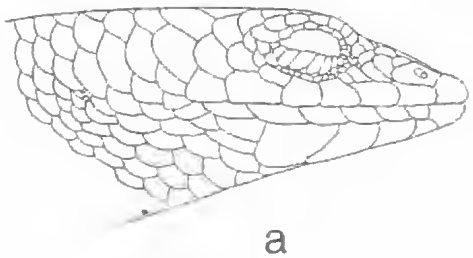
E. Lower labial scales. Most generally primitive *Eugongylus* group species have 6 lower labials which is considered the primitive condition (E). Reduction in the number of lower labials, is considered to be derived (e).

N. maccoyi, *N. gracilis* , and *N. sleveni* have the primitive condition of 6 lower labial scales, while *N. mariei*, *N. greeri* and *N. rankini* have 5 lower labials (e).

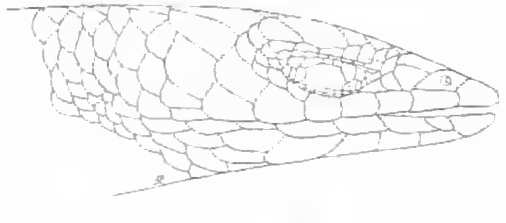
F. Lower eyelid morphology. A scaled lower eyelid is considered primitive for lygosomine skinks, and derivations from this condition derived.

The lower eyelid of *N. maccoyi*, *N. greeri* (Fig. 2b) and *N. rankini* has a semi-transparent disc below a distinct palpebral rim. *N. mariei*, *N. gracilis* and *N.sleveni* (Fig. 2a and 2c) lack sutures defining the palpebral rim and have the opaque central area of the lower eyelid divided by fine transverse sutures only ('scaled').

It is however unclear whether these conditions



a



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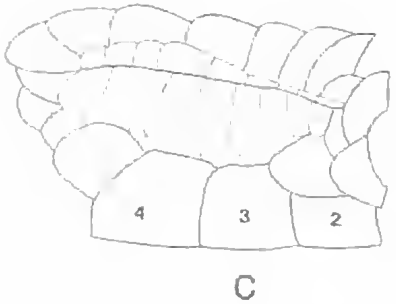

c

FIG. 2. Lateral view of the head of: (a) *N. sleveni* with the lower eyelid in the raised position showing the 'scaled' lower eyelid typical of *N. gracilis*, *N. sleveni* and *N. mariei*; (b) *N. greeri* with the lower eyelid in the raised position showing the windowed condition typical of *N. maccoyi*, *N. greeri*, and *N. rankini*; (c) detail of the scalation of (a) above.

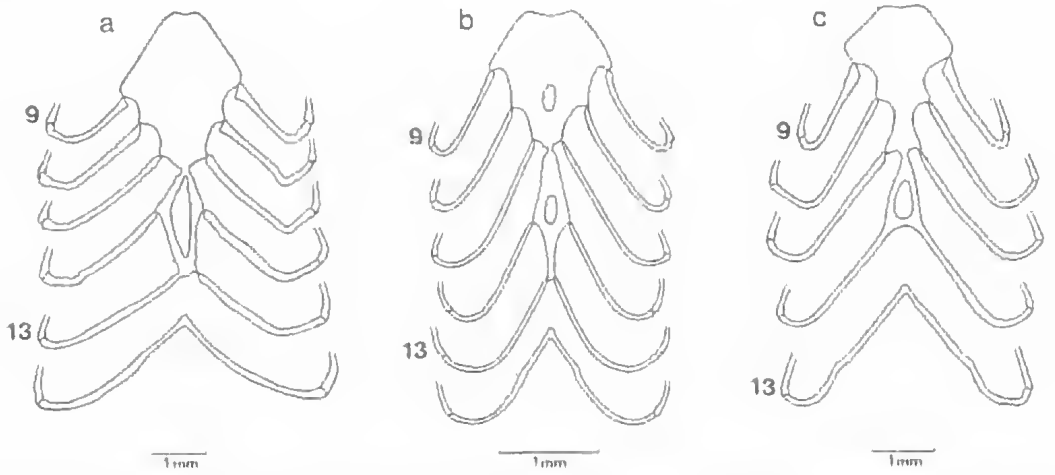

FIG. 3. The various types of mesosternal rib attachment found in the *Nannoscincus* subgroup: (a) *N. maccoyi*; (b) *N. mariei*, typical of *N. mariei* and *N. greeri*; (c) *N. gracilis*, typical of *N. gracilis*, *N. sleveni*, and *N. rankini*.

(above) for *Nannoscincus* represent: 1) 2 independent patterns of evolution from an ancestor with the scaled condition. 2) the 'scaled' condition is secondarily derived from an ancestor having a semi-transparent disc in the lower eyelid. 3) the lower eyelid with a semi-transparent disc is derived from an ancestor with a 'scaled' lower eyelid. For this reason polarities have not here been assigned to either of the conditions.

Of the above possibilities the most parsimonious would be the 2nd, with the apparent loss of the palpebral sutures defining the palpebral rim and reaquisition of fine, widely spaced, transverse sutures possibly the result of an extension of the palpebral rim down over the centre of the eye to its lower margin, from an ancestor with a semi-transparent disc.

G. Mesosternal rib attachment. Contact of the 12th and 13th ribs with the mesosternum is considered the primitive condition (G). Loss of the 13th rib attachment to the mesosternum (g) is considered to be the derived condition.

The primitive condition exists in *N. maccoyi* (Fig. 3a) and in a slightly modified form in *N. mariei* and *N. greeri* (Fig. 3b), whereas *N. rankini*, *N. gracilis* and *N. sleveni* have the 12th rib only contacting the mesosternum (g) (Fig. 3c), and the 13th rib lying posterior and separate to the mesosternum.

H. Phalangeal formula of the manus. The primitive phalangeal formula for the manus is 2.3.4.5.3. Loss of phalanges on the manus is a derived condition. The phalangeal formula for the manus of the ancestor of *Nannoscincus* is considered to be 2.3.4.4.3 (H), and is the condition occurring in *N. maccoyi*, *N. greeri*, *N. rankini* and *N. mariei*. Loss of an additional phalange on the 3rd and 4th digits of the manus of *N. gracilis* (2.3.3.3.2) and *N. sleveni* (2.3.3.3.0) is considered derived (h) within the genus. Note the phalangeal formula for *N. sleveni* given previously by Sadlier (1987) was incorrect (read in reverse off x-ray plate) and is here corrected to a loss of the 5th (rather than 1st) digit - a condition unique within the Eugongylus group.

I. Phalangeal formula of the pes. The primitive phalangeal formula for the pes is 2.3.4.5.4. (I), and reduction in phalange number derived (i).

N. greeri, has the primitive phalangeal formula. The phalangeal formula for the remaining species of *Nannoscincus* is 2.3.4.4.3. Loss of a phalange on the 4th and 5th digits of the pes of these species is considered derived within the genus.

J. Presacral vertebrae. In skinks the modal number of presacral vertebrae is 26, any deviations from this can be taken as progressive derivations. The species with the lowest number of vertebrae above 26 will be primitive for this condition, and those with a higher number of vertebrae derived.

In *Nannoscincus* presacral vertebrae number is variable but falls roughly into 2 groups: *N. mariei* (31-32, mode 31), *N. greeri* (29) and *N. rankini* (29-30) with generally 31 or fewer presacral vertebrae which is considered primitive (J) for the genus; and *N. maccoyi* (34-37), *N.*

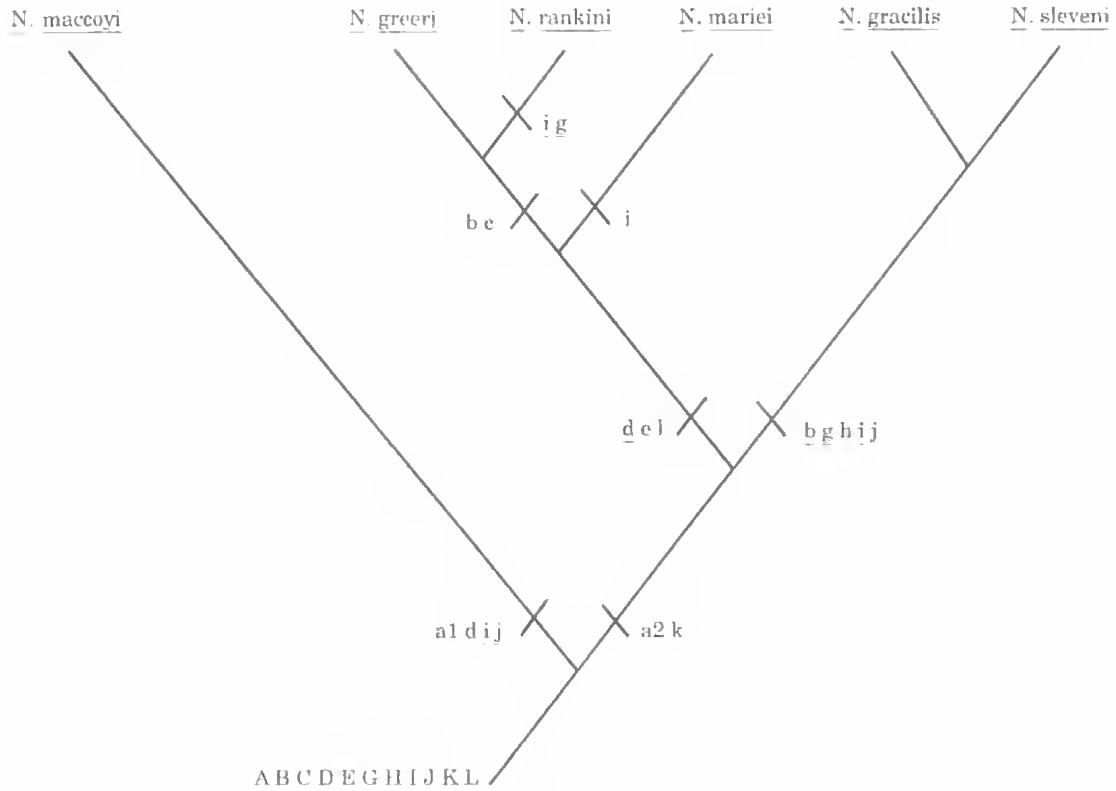

FIG. 4. Phylogeny of the genus *Nannoscincus* subgroup.

sleveni (31-34, mode 32) and *N. gracilis* (33-34) with generally 32 or more presacral vertebrae which is derived (j) within the genus.

K. Atlantal vertebrae. In most generally primitive lygosomine skinks the atlas consists of 3 distinct elements, the 2 atlantal arches and the intercentrum.

All species of *Nannoscincus* have the atlantal arches fused to the intercentrum. *N. maccoyi* has the atlantal arches distinct dorsally where they abut, this is considered the primitive condition (K) within the genus. The remaining species of *Nannoscincus* have undergone further fusion of the atlantal vertebrae, the atlantal arches being fused to one another dorsally, this is derived (k) for the genus.

L. Oviduct. The presence of a pair of oviducts in females is considered the primitive condition (L) and occurs in *N. maccoyi, N. gracilis* (*bar 1 specimen see below), and *N. sleveni*. A single oviduct only occurs on the right side of the body in *N. mariei* and *N. greeri*, and is the derived condition (l).

N. rankini is known only from 2 adult male specimens, the female reproductive trait for this species is therefore unknown.

A single female *N. gracilis* examined had a single oviduct on the right side of the body containing a single enlarged yolked ovarian follicle. This individual is unusual in 2 other respects. Firstly it is the smallest reproductively active female *N. gracilis* examined, and secondly it is from a geographically disjunct point in the species range. At this stage it is unclear as to whether this specimen represents an aberrant individual of *N. gracilis*, or a sibling species to *N. gracilis* distinguished solely on the oviduct condition. If the latter it would represent another case of loss of the left oviduct.

M. Ventral coloration. The polarity of features of coloration are uncertain, however they may in the future add to our knowledge of relationships.

The venter of *N. maccoyi* in life has an orange flush predominantly in males and a yellow flush in females. No orange or yellow flush to the venter was observed in live (breeding and non-breeding) *N. mariei, N. gracilis, N. sleveni* or *N. rankini* I have observed.

TABLE 1. Summary of distribution of character states within *Nannoscincus*. Polarities are denoted by capital letters for the primitive condition and lower case for the derived condition.

Character States	*N. maccoyi*	*N. greeri*	*N. mariei*	*N. rankini*	*N. gracilis*	*N. sleveni*
a1 prefrontals fused a2 prefrontals diminutive	a1	a2	a2	a2	a2	a2
B frontal not contacting 1st supraciliary b frontal contacting 1st supraciliary	B	b	B	b	b	b
C frontoparietal scales paired c frontoparietal scales fused	C	c	C	c	C	C
D loreal scales 2 d loreal scales 1	d	d	d	d	D	D
E lower labial scales 6 e lower labial scales 5	E	e	e	e	E	E
F? lower eyelid 'scaled' lower eyelid windowed	window	window	'scaled'	window	'scaled'	'scaled'
G mesosternal ribs 12 + 13th g mesosternal ribs 12th only	G	G	G	g	g	g
H phalanges of manus 2.3.4.4.3 h phalanges of manus 2.3.4.4.2	H	H	H	H	h	h
I phalanges of pes 2.3.4.5.4 i phalanges of pes 2.3.4.4.3	i	I	i	i	i	i
J presacral vertebrae 31 or less j presacral vertebrae 32 or more	j	J	J	J	j	j
K atlantal arches distinct k atlantal arches fused	K	k	k	k	k	k
L oviducts paired l oviduct single	L	l	l	?	L	L
M? ventral colouration present ventral colouration absent	present	?	absent	absent	absent	absent

RELATIONSHIPS WITHIN *NANNOSCINCUS*

The most parsimonious phylogenetic interpretation drawn from these characters proposes an initial dichotomy between the Australian species *N. maccoyi* and the remaining New Caledonian species of *Nannoscincus*. The New Caledonian *Nannoscincus* are diagnosed by the derived character state (k) atlantal arches fused dorsally; while the Australian species *N. maccoyi* is diagnosed by the unique contact between the frontal and premaxilliary bones given in the subgeneric diagnosis below. Interpreting loss of prefrontals in *N. maccoyi* (a1), and the diminutation of prefrontals in the New Caledonian *Nannoscincus* (a2) as 2 independently derived patterns of reduction would further identify this basic dichotomy in *Nannoscincus*. Similarly presence or absence of ventral coloration, depending on the polarity of the character states, would further diagnose either *N. maccoyi* or the New Caledonian *Nannoscincus* as monophyletic subgenera.

Between these proposed subgenera is inferred parallel evolution in the following characters: (d) reduction to a single loreal in that region between *N. maccoyi* and *N. mariei* + *N. rankini* + *N. greeri*; (i) loss of a phalange on the 4th and 5th digits of the pes between *N. maccoyi*, and *N. mariei*, *N. rankini*, and *N. gracilis* + *N. sleveni* to infer 4 independent occurrences of this character evolving; (j) increased number of presacral vertebrae between *N. maccoyi*, and *N. gracilis* + *N. sleveni*; and the windowed lower eyelid between *N. maccoyi* and, *N. greeri* + *N. rankini*, if it is considered to have evolved from a primitively scaled or 'scaled' lower eyelid.

Diagnosis for the proposed subgenera within *Nannoscincus* are given below.

Subgenus **Nannoscincus** Günther

Anotis Bavay, 1869: 29 (type species *Anotis mariei*, Bavay, 1869).

Nannoscincus Günther, 1872: 421 (type species *Nannoscincus fuscus*, Günther, 1872 = *Nannoscincus mariei*).

TYPE SPECIES

As for genus.

DIAGNOSIS

The species here included in the subgenus *Nannoscincus* can be distinguished from other *Eugongylus* group genera by sharing the following combination of derived characters : atlantal arches fused dorsally; loss of a single phalange in the 4th digit of the manus (2.3.4.4.3 for *N. greeri*, *N. rankini* and *N. mariei*, further reduced to 2.3.3.3.2 in *N. gracilis* and 2.3.3.3.0 in *N. sleveni*); ear opening reduced or completely scaled over; supranasals absent; prefrontals small to diminutive and widely separated, or absent; upper labials 6; single pair of enlarged nuchals.

DISTRIBUTION

New Caledonia.

Subgenus **Nannoseps** n. subgen.

TYPE SPECIES

Saiphos maccoyi, Lucas and Frost, 1894).

DIAGNOSIS

The monotypic subgenus *Nannoseps* can be distinguished from other *Eugongylus* group genera by the following combination of derived characters: frontal bone contacting premaxilliary thereby excluding contact between nasals: loss of a single phalange in the 4th digit of the manus (2.3.4.4.3); loss of a single phalange in the 4th and 5th digits of the pes (2.3.4.4.3); ear opening reduced; supranasals absent; prefrontals absent; upper labials 6; single pair of enlarged nuchals.

DISTRIBUTION

Southeastern Australia.

ETYMOLOGY

Nannoseps is derived from the Greek 'nannos' meaning dwarf or little, and the Latin 'seps' for lizard.

RELATIONSHIPS WITHIN THE SUBGENUS *NANNOSCINCUS*

Within the subgenus *Nannoscincus* the most parsimonious interpretation proposes an initial dichotomy between the species *N. mariei* + *N. rankini* + *N. greeri* (the *N. mariei* species group), and the species *N. gracilis* + *N. sleveni* (the *N. gracilis* species group).

The *N. mariei* species group is diagnosed by the derived characters: (d) a single loreal scale; (e) reduction to 5 lower labials; and tentatively (l) loss of the left oviduct. The *N. gracilis* species group is diagnosed by the derived characters: (h) loss of an additional phalange on the 3rd and 4th

digits of the manus; (j) a presacral vertebrae number of generally 32 or more.

This initial subdivision infers parallel evolution of character states in: (b) the 1st supraciliary scale contacting the frontal between *N. greeri* + *N. rankini*, and *N. gracilis* + *N. sleveni*; (g) the 12th rib only contacting the mesosternum between *N. rankini*, and *N. gracilis* + *N. sleveni*; (i) loss of a phalange on the 4th and 5th digits of the pes between *N. mariei*, *N. rankini*, and *N. gracilis* + *N. sleveni*; and the 'scaled' lower eyelid between *N. mariei* and the *N. gracilis* species group if it is considered to have evolved from an ancestor with a primitively scaled or windowed lower eyelid.

COMMENTS

The majority of scincid genera (ie. 7 of 10 recognised by Sadlier, 1987) occurring in New Caledonia are either endemic to the main island (*Geoscincus*, *Graciliscincus*, *Marmorosphax*, *Tropidoscincus*, *Sigaloseps*) or only extend outside the main island east to the nearby Loyalty Islands (*Phoboscincus*, *Caledoniscincus*). Those species restricted to mainland New Caledonia usually occur in moist closed forest habitats (only the species of *Tropidoscincus* occur in open habitat), while the endemic New Caledonian genera with representatives on the Loyalty Islands tend to be habitat generalists. Species assigned to *Leiolopisma* by Sadlier (1987) comprise a residue of essentially primitive *Eugongylus* group species whose relationships are obscure. While they cannot at present be placed with certainty within existing monophyletic genera they may eventually be diagnosed as endemic New Caledonian taxa. The strength of the context within which *Nannoscincus* is placed, i.e. within a subgroup of *Eugongylus* group species having the atlantal arches fused to the intercentrum, lies in the occurrence of this character in both surface active and semifossorial or burrowing species. Its presence in the former infers it evolved other than as a modification to a subsurface mode of existence, unlike phalange reduction and/or increase in presacral vertebrae number which have evolved a number of times and are variably expressed in burrowing lineages of skinks. The phylogeny here proposed for the species of *Nannoscincus* presents a scheme of relationships inferring the least number of cases of parallel evolution of characters, and identifies the New Caledonia *Nannoscincus* as a discrete geographical unit. However, these groups or lineages so far defined within *Nannoscincus*, are based on two or less derived characters for which no instance of parallel evolution is inferred, and usually a further 1-4 characters for which one or more instance of parallel evolution is inferred.

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